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A mechanistic model of climate change risk: Growth rates and microhabitat specificity for conservation priority woodland epiphytes

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ABSTRACT

Climate change studies need to develop models for species risk that are mechanistic and predictive, with conservation strategies explored through the use of scenarios. This study focused on a diverse group for climate change analysis – lichen epiphytes – to develop a heuristic model for quantifying risk that has two key components. First, it draws on the classic ecological concept – '*das Gesetz der relativen Standortskonstanz*' – which explains how the suitable niche space of a species (at a microhabitat-scale) may occur under different local circumstances in contrasting macroclimatic zones. To quantify this pattern, conservation priority cyanolichen and tripartite epiphytes were sampled across a steep climatic gradient, to characterise their different microhabitat preferences in optimal and sub-optimal macroclimates. Second, the model used climatically controlled growth rates as a functional response to climate variability, leading to an increase in generation time for sub-optimal climates. Together, the macroclimate-microhabitat and growth rate data parameterise a mechanistic population model that was used to explore the effect of environmental change scenarios, including: 1. Climate change leading to longer generation times, and 2. A reduction in habitat quality, e.g. through a tree disease scenario such as ash dieback. The advantage of this population approach was its down-scaling to better understand a species' local vulnerability. Accordingly, the study suggested how management at landscape or habitat-scales can be used to offset the negative effects of climate change. Because extinction rates for the epiphyte populations are low, and established individuals are relatively long-lived, there is a time-lag during which conservation can increase the resilience of threatened populations. However, multiple threats, such as climate change and tree disease combined, severely shorten this window of opportunity.

1. Introduction

Managing the risk to biodiversity of human-induced climate change is a major challenge for conservation (Sala et al., 2000). A large body of work has examined the species response to climate change using bioclimatic models (Pearson and Dawson, 2003; Peterson et al., 2011). According to concepts of risk management borrowed from the insurance industry (Crichton, 1999; Ellis, 2013), this approach estimates the 'exposure' of a species to the climate change 'hazard', by measuring species sensitivity to the magnitude of climate change, e.g. as the loss of, or degree of spatial change in suitable climate space (Thomas et al., 2004; Loarie et al., 2009). However, the overall risk to a species depends also on 'vulnerability'. Habitat loss and fragmentation are well-researched examples of vulnerability factors, with two effects dependent on species biology: 1. Reduced migration ability to track suitable climate space (Schwartz, 1992; Honnay et al., 2002), as well as 2. Reduced size and resilience of populations (Maschincki et al., 2006; Lawson et al., 2010), eroded genetic diversity (Frankham, 1996; Honnay and Jacquemyn, 2007), and limited potential for evolutionary adaptation (Jump and Peñuelas, 2005). Once understood, vulnerability factors such as habitat loss and fragmentation can be managed at a landscape scale, by ensuring that the spatial pattern of habitat allows for an evolutionary (Hoffman and Sgrò, 2011; Sgrò et al., 2011) and ecological response (Pressey et al., 2007) commensurate with a species' exposure. Considering vulnerability (in addition to exposure) directs thinking from large-scale biogeographic patterns (bioclimatic models), towards local evolutionary/ecological processes with a more direct functional basis (population size and isolation, genetic diversity and gene flow) that can be used to identify practical options in conservation management.

Complimentary to habitat loss and fragmentation, habitat quality is a vulnerability factor also relevant to climate change risk (Hodgson et al., 2009). A species' relationship with habitat quality is spatially and temporally dynamic. The classic concept of '*das Gesetz der relativen Standortskonstanz*' (Walter and Walter, 1953; Poelt, 1987) explains how the suitable niche space of a species (at a microhabitat-scale) may occur

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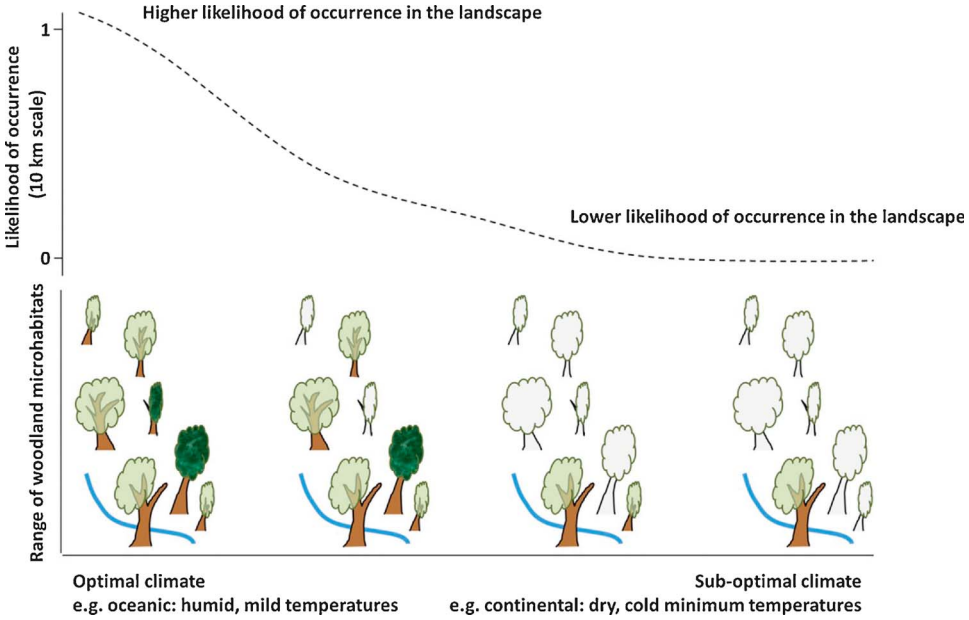
Higher likelihood of occurrence in the landscape
1
Likelihood of occurrence (10 km scale)
0
Lower likelihood of occurrence in the landscape
Range of woodland microhabitats
Optimal climate
e.g. oceanic: humid, mild temperatures
Sub-optimal climate
e.g. continental: dry, cold minimum temperatures

Fig. 1. Schematic to show how a species occurrence in woodland microhabitat may vary along a macroclimatic gradient: cf. '*das Gesetz der relativen Standortskonstanz*'. In an optimum climate, a wide cross-section of the available microhabitat might provide suitable niche conditions for species occurrence (coloured habitat symbols), e.g. in an oceanic climate zone equating to a minimum of moisture or warmth. Moving towards a sub-optimal climate, microhabitats may fail to meet threshold niche conditions (greyed habitat symbols) leading to species occurrence in a smaller cross-section of the available microhabitat (narrower microhabitat specificity), e.g. older trees and/or those closer to watercourses. Allowing for trends in microhabitat heterogeneity, this would translate into a shift from more to fewer landscape occurrences (e.g. records in 10 km grid squares), and a decreasing likelihood of occurrence in coarse-grained bioclimatic models. Nevertheless, suitable microhabitat may continue to occur as isolated refugia within sub-optimal climates. Thus, in a temporal climate change scenario, quantifying and then proactively managing this interaction of macroclimate-microhabitat specificity could provide a key tool for reducing species vulnerability.

under different local circumstances in contrasting macroclimatic zones. Thus, within an optimal climate, a larger proportion of available microhabitat may meet the condition for species occurrence (broad microhabitat specificity), while under a sub-optimal climate suitable niche space may coincide with a narrower proportion of the available microhabitat, thus increasing the degree of microhabitat specificity (Fig. 1). If particular microhabitats provide locally suitable microclimatic conditions, despite a sub-optimal macroclimate, they become analogous to 'microrefugia' (Rull, 2009; Dobrowski, 2010). This cross-scale interaction observed spatially (macroclimate-microhabitat specificity) provides a powerful opportunity for conservation, e.g. if suitable microhabitats can be purposefully augmented to offset a temporal shift from an optimal to sub-optimal climate.

This study focused on an ecosystem for which poor habitat quality has been identified as the key risk factor, i.e. woodlands (Mace et al., 2015), and an ecological guild that is strongly affected by manageable aspects of woodland quality, i.e. epiphytes (Ellis, 2012). Taking oceanic 'temperate rainforest' epiphytes as a high priority example for conservation (DellaSala, 2011; Ellis, 2016), previous studies have indicated that these moisture-dependent and cold-intolerant species demonstrate shifts in microhabitat specificity as one transitions from climatically optimal oceanic through to sub-optimal climatic zones (Goward, 1995; Lidén and Hilmo, 2005) particularly at climate thresholds such as range-margins (Lisewski and Ellis, 2010). This microhabitat specificity scales-up to explain a transition from broad habitat occupancy in optimal climates, through to an increasing association with ancient woodland or old-growth-like forest habitats in sub-optimal climates (Goward, 1994). Accordingly, it has been shown that old-growth forest may provide a more humid environment for a given macroclimatic regime (McCune and Antos, 1982) with greater microhabitat heterogeneity leading to – on average – the increased availability of different (and potentially suitable) microclimatic niche space, compared to the simplified structure of managed woodlands (Lesica et al., 1991; Michel and Winter, 2009). An aim of this study was to quantify this spatial pattern of macroclimate-microhabitat specificity, and to explore how this might be deployed in a temporal framework. This can help understand how woodland management might offset the negative consequences of climate change (Ellis, 2013), for example through regeneration targeted to nodes of European 'ancient woodland' (Ellis et al., 2009) and reconstitution of its old-growth structure.

However, the associated occurrence/abundance of oceanic epiphytes in ancient woodland/old-growth forest stands, for sub-optimal climates, might invoke not only the limiting effect of suitable microhabitat (refugia), but also the time-for-colonisation with increasing stand-age (Peterson and McCune, 2001) given constraints imposed by dispersal-limitation (Dettki et al., 2000; Sillett et al., 2000). Epiphytes have a climatically controlled growth response (Gaio-Oliveira et al., 2004; Gauslaa et al., 2007), and lower growth rates and longer generation times in sub-optimal climates may reduce fecundity. The production of fewer propagules per population would lower rates of colonisation and skew occurrences to microhabitats that have existed in the landscape over longer time-periods, i.e. with higher accumulated colonisation probabilities.

To synthesise the relationship between macroclimate-microhabitat specificity (niche response) and climatically controlled growth rates (fecundity), relevant to climate change risk, this study builds on a population simulation (Ellis, 2017) that is applied here to oceanic epiphytes in the cyanolichen and tripartite functional guild (Ellis, 2013; Rikkinen, 2015). These are lichens whose fungal component is associated with cyanobacteria as their primary photobiont partner, or alternatively with green-algae and with cyanobacteria performing a nitrogen-fixing function, respectively. The study is developed as a heuristic tool, but provides two important developments over the standard bioclimatic approach, as it has been applied to lichens (Ellis et al., 2007a,b): 1. The response to climate based on growth rates provides a more robust functional basis than correlative bioclimatic studies (Eaton and Ellis, 2012; Ellis et al., 2017), and 2. It allows an understanding of how the vulnerability component of climate change risk might be managed through actions to augment local microhabitat quality. Climate change risk is thus presented in a mechanistic and predictive framework that can engage with multiple threats and solutions.

2. Methods

2.1. Field sampling

The study utilised a large field-sampled dataset from a survey of lichen epiphyte communities across Scotland: see Ellis et al. (2015a) for details. A total of 1013 quadrats were sampled randomly from 250 trees in 20 woodland sites, positioned along a steep climatic gradient from the oceanic west through to the more continental northeast (Fig. 2). Scotland has a very strong rain-shadow effect over a relatively short longitudinal distance, providing an ideal situation to explore climate

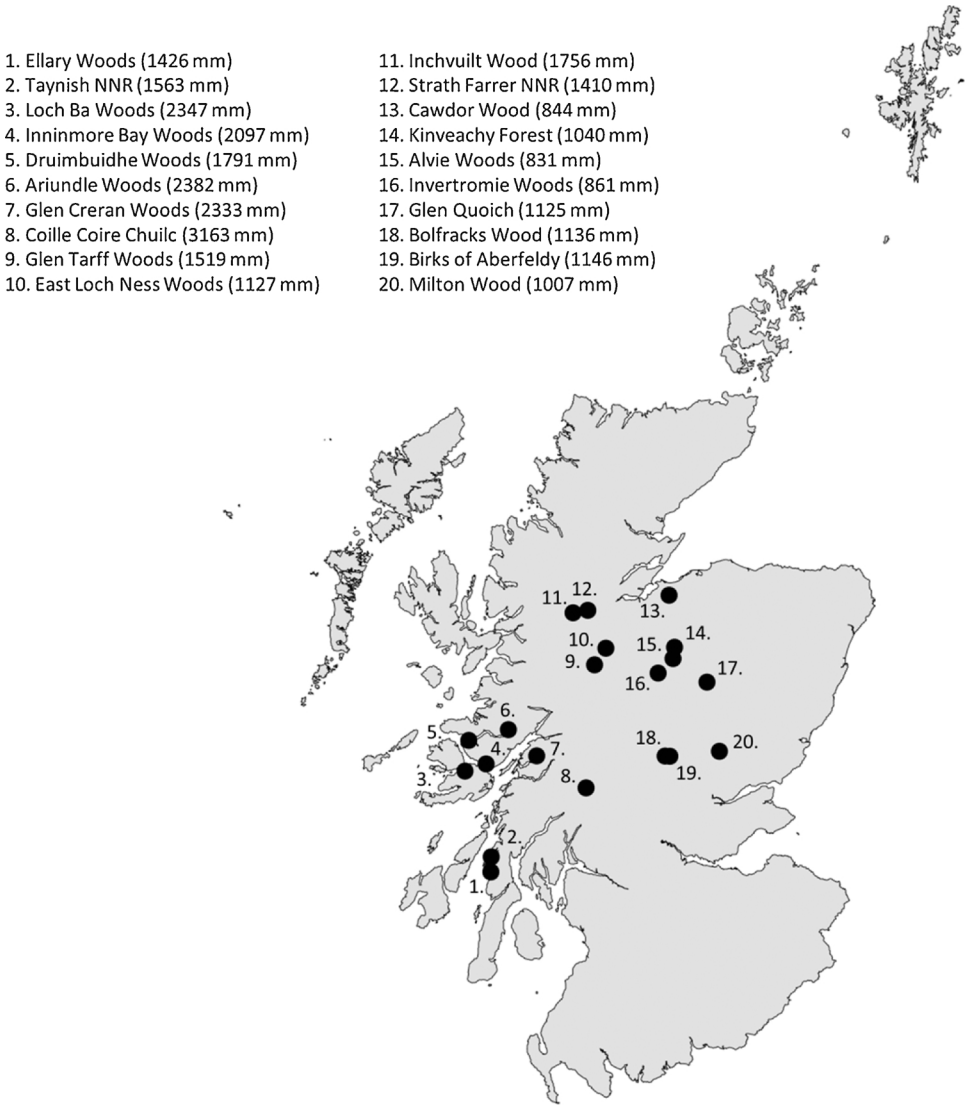
1. Ellary Woods (1426 mm)
2. Taynish NNR (1563 mm)
3. Loch Ba Woods (2347 mm)
4. Inninmore Bay Woods (2097 mm)
5. Druimbuidhe Woods (1791 mm)
6. Ariundle Woods (2382 mm)
7. Glen Creran Woods (2333 mm)
8. Coille Coire Chuilc (3163 mm)
9. Glen Tarff Woods (1519 mm)
10. East Loch Ness Woods (1127 mm)
11. Inchvuilt Wood (1756 mm)
12. Strath Farrer NNR (1410 mm)
13. Cawdor Wood (844 mm)
14. Kinveachy Forest (1040 mm)
15. Alvie Woods (831 mm)
16. Invertromie Woods (861 mm)
17. Glen Quoich (1125 mm)
18. Bolfracks Wood (1136 mm)
19. Birks of Aberfeldy (1146 mm)
20. Milton Wood (1007 mm)

Fig. 2. The distribution of 20 woodland study sites in Scotland (with their annual precipitation), used for sampling lichen epiphyte communities (Ellis et al., 2015a) and here modelling the climate and microhabitat response of cyanolichen and tripartite species.

sensitivity. Sites in western Scotland receive > 3000 mm precipitation per year, and have consistently above-zero mean minimum winter temperatures, corresponding to a temperate rainforest bioclimatic zone (Alaback, 1991; DellaSala, 2011). In contrast, sites in north-eastern Scotland receive < 1000 mm rainfall per year, with sub-zero mean minimum winter temperatures in a relatively continental climatic setting.

Sampling of woodland sites aimed to capture the breadth of epiphytic niche space, i.e. targeting trees of different species, in multiple size classes, for different topographic positions (Ellis et al., 2015a). For the purposes of this study, the data were reduced to the presence-absence of cyanolichen and tripartite species in each quadrat.

2.2. Niche modelling

The aim was to generate two different niche models relating to the oceanic 'optimal' and relatively more continental 'sub-optimal' portions of the climatic gradient. To differentiate between optimal and sub-optimal climatic zones, the proportion of trees occupied by cyanolichen or tripartite epiphytes at each woodland site was calculated, and compared to interpolated values (5 km scale) in mean annual precipitation (mm), for the period 1961–2006 (Perry and Hollis, 2005). The extended time-period is used to avoid anomalies in spatial climatic trends that might be associated with any individual year, and to ensure that climate comparison is compatible with the baseline time-period used for recent bioclimatic modelling (Ellis et al., 2014a, 2015b). Spatial variability in the climate (oceanic v. continental) is expected to be consistent over the baseline period, despite recent warming (Jenkins et al., 2009). A threshold in the cyanolichen and tripartite species response was identified by splitting the woodland sites into two groups, and using consecutive points along the climatic gradient to form these pairwise-groups multiple times. The pairwise-groups were tested by resampling the proportion of occupied trees from within each of the two groups (10,000 randomisations), and comparing their values using a *z*-test to calculate significance (*P*). It was possible to identify a climatic threshold at a point where the difference in lichen occupancy among site groups was maximised, i.e. lowest *P* value, minimum *z*. Given a known sensitivity of cyanolichen and tripartite species to temperature, we also explored the correlation between annual precipitation and mean temperature of the coldest month (°C).

Having established optimal and sub-optimal climatic zones, the quadrat-scale response of cyanolichen and tripartite epiphytes was modelled as presence-absence, using nonparametric multiplicative regression (NPMR: McCune, 2006). This method explored potentially complex interactions among microhabitat variables relevant to tree-scale dynamics: tree species identity, tree age and size (girth at 1.3 m),

aspect and height on the tree bole, angle of bole lean, furrow depth and bark roughness, bark pH and conductivity, bark water capacity and density and the presence-absence of bryophytes: see Ellis et al. (2015a) for details. A full description of NPMR is provided by McCune (2011); we used 'medium' model building defaults implemented in Hyperniche v. 2 (McCune and Mefford, 2009), with a Gaussian smoother to fit a response curve. The optimum NPMR model fit (highest log*B* for a binary response) was tested for significance using a permutation test with 250 randomisations.

Using the NPMR niche response, a threshold for detecting suitable/unsuitable microhabitat was the minimum likelihood value for any sample in which a species was confirmed present, i.e. the 'least training presence' (Peterson et al., 2011). Applied to the quadrats grouped across sites within each climatic zone (optimal and sub-optimal), the threshold was used to calculate: 1. The proportion of suitable microhabitat that was occupied by a species (abbreviated as *P*'), 2. The proportion of suitable microhabitat that was unoccupied by a species, and 3. The proportion of unsuitable microhabitat.

2.3. Population simulation

A previously published population model was adapted to simulate ecological dynamics across a series of annual time steps (t_x), and to measure the proportion of microhabitat occupied (*P*') as an outcome: see Ellis (2017) for technical details, and examples in Appendix A.

The simulation consisted of a woodland 'patch' (woodland site or stand) with a fixed number of microhabitat units (*H*), which for epiphytes can be considered as trees, with $H = 10{,}000$. A carrying capacity (*K*) determined the proportion of these units suitable for establishment, and a disturbance rate (*E*) forced the extinction of these including any established epiphytes, followed by a process of microhabitat regeneration to maintain the value *K*. Assuming each microhabitat unit could be colonised by a single 'individual' epiphyte, there were two population parameters. The generation time (*Gt*) set the age at which an established epiphyte becomes reproductively active, and the colonisation rate (*Cl*) yielded the number of propagules produced per reproductive epiphyte per time step (i.e. for an epiphyte where age $\geq Gt$) that colonise into microhabitat units.

The number of colonising propagules (*M*) was determined as the sum of two values, M_L (local origin propagules) and M_R (immigrant propagules). Thus, M_L is calculated as the number of established epiphytes that had achieved an age threshold for reproduction (age $\geq Gt$), multiplied by the colonisation rate (*Cl*). Additionally, M_R is the number of propagules colonising into microhabitats though originating from outside the woodland patch, and was determined as the number of local origin propagules (M_L) multiplied by a correction factor ($_mP$) that represented landscape connectivity. M_R is thus equivalent to the metapopulation colonisation of empty patches, or the 'rescue effect' for extant populations (Brown and Kodric-Brown, 1977; Hanski, 1982, 1999). Propagules (*M*) were dispersed randomly among the microhabitat units, with colonisation leading to successful establishment for propagules which associated with unoccupied suitable microhabitat, failing in all other cases (occupied suitable microhabitat, or unsuitable microhabitat).

The correction factor $_mP$ was based on a simple assumption that the density of propagules would decline at distance from source to sink (target woodland patch), as a function of circumference (dilution) given a radius equal to the linear source-sink distance. This represents the merging of a distance decay property into a general 'background' value for long-distance dispersal, which is shown to be ecologically meaningful in explaining epiphyte colonisation patterns at landscape-scales (Gjerde et al., 2015). The value of $_mP$ was calculated by assuming that extant ancient woodlands represent the most likely source of propagules for the cyanolichen and tripartite epiphytes in Scotland's landscape (Coppins and Coppins, 2002; Whittet and Ellis, 2013). Using digitised polygons for Class 1a ancient woodland in Scotland (woodlands having existed ≥ 260 yr: Roberts et al., 1992), the distance from all sources (all ancient woodlands) to each sink (each field sampled woodland used for niche modelling: see *Field Sampling*, above) was measured using ArcMap v. 10 (ESRI, Redlands, California). The individual source-sink values of $_mP$ were calculated and summed, and then expressed as a mean for woodland sites grouped within optimal and sub-optimal climatic zones. To reflect a relevant spatial scale for declining propagule density, the source-sink distances were expressed in metres (Öckinger et al., 2005; Werth et al., 2006). Finally, $_mP$ was standardised, so that $_mP = 1$ only for a contiguous wooded landscape, i.e. emigration will be balanced by immigration when there is 100% woodland cover.

For analytical simplicity, two configurations of the carrying capacity (*K*) were matched to the proportion of suitable microhabitat in optimal and sub-optimal climatic zones (see *Niche Modelling*, above), set at $K = 0.8$, and $K = 0.475$, respectively. The age at which individuals reach reproductive maturity (*Gt*) was assumed to be under climatic control. On this basis, a value for the optimal climatic zone (9 years) was the estimated average age of the tripartite lichen *Lobaria pulmonaria* at reproductive maturity (production of asexual diaspores) in oceanic western Scotland (Eaton and Ellis, 2014). Similar short generation times having been reported from temperate rainforest systems in south-west Norway (Høistad and Gjerde, 2011) and British Columbia (MacDonald and Coxson, 2013). These contrasted with two values corresponding to longer generation times applied within the sub-optimal climatic zone (20 or 35 years), based on upper and lower estimates for *Lobaria pulmonaria* in the relatively more continental climate of central Europe (Scheidegger et al., 1998; Scheidegger and Goward, 2002).

The extinction rate *E* was applied as a combination of deterministic and stochastic disturbances causing an annual rate of epiphyte loss, and similar to values previously reported for cyanolichen and tripartite species (Fedrowitz et al., 2012): 1. The deterministic loss of microhabitat is through tree death estimated at c. 2% per year for European temperate forests (Peterken, 1996; Drobyshev et al., 2009), combined with 2. A stochastic loss rate from extant trees estimated at 2.5% per year, for patches of *Lobaria pulmonaria* based on observations over a 10 year period in southern Sweden (Öckinger and Nilsson, 2010). The disturbance rate was therefore set at $E = 0.045$, or 4.5% of microhabitat units per time step.

Finally, the colonisation rate (*Cl*) was estimated, so that the proportion of microhabitat observed to be occupied in the simulation (*P*') converged over a transient period of 1000 time steps to match with the proportion of suitable microhabitat occupied under field conditions (see *Niche Modelling*, above) for the two climatic zones (optimal and sub-optimal). Setting $E = 0.045$, and with each of three unique combinations of *K* and *Gt* (optimal climate: $K = 0.8$, $Gt = 9$; sub-optimal climate faster growth: $K = 0.475$, $Gt = 20$; sub-optimal climate slower growth: $K = 0.475$, $Gt = 35$), the population model was run for combinatorial values of $_mP$ and *Cl*, each with 100 repeat simulations, to estimate the mean ± 1 SD in values of *P*' at t_{1000}. First, these values were interpolated to explain how *P*' varies as a function of *Cl*, and this was used to understand how *Cl* and $_mP$ must interact to maintain the field condition *P*' observed for the two climatic zones (optimal and sub-optimal). Second, adopting values of *Cl* consistent with $_mP$ observed for Scotland's landscape (based on the known extent of ancient woodland, see above), the effect of microhabitat continuity was tested by comparing the microhabitat age for newly established thalli among the contrasting optimal and sub-optimal climate zones, using a Kruskal-Wallis test.

2.4. Risk scenarios in the optimal climatic zone

Three environmental change scenarios were investigated for the optimal climatic zone. Each was implemented following the transient period of 1000 time steps (at t_{1001}), to explore the population response

from t_{1001} to t_{2000}.

- **Experiment 1:** The growth rate was reduced in order to increase the generation time (*Gt*) from 9 years by an additional 5 years (*Gt* = 14 years), or to *Gt* = 20 or 35 years (consistent with growth under a more continental climate, see *Population Simulation*, above), and estimating the effect on the population size.
- **Experiment 2:** Following the increased *Gt* in Experiment 1 (e.g. *Gt* shifting from 9 to 14 years), at t_{1001}, two management options were implemented: 1. Increasing the availability of suitable microhabitat (*K*), after 50 years, at t_{1051}, consistent with the expected length of time for management interventions to diversify stand structures, or 2. Increasing the rescue effect ($_mP$) after 200 years, at t_{1201}, consistent with the time-frame for landscape restoration of woodland.
- **Experiment 3:** In addition to the increased *Gt* for Experiment 1, the amount of suitable microhabitat was reduced, from the original value of *K* = 0.8, through to *K* = 0.6, 0.4 and 0.2, in order to estimate the effect of declining habitat quality on population size, alongside a reduced growth rate.

3. Results

A total of 30 species were sampled from the cyanolichen and tripartite epiphyte guild (Table A in Supplementary material). A threshold in the proportional occurrence of these species was determined at a mean annual precipitation of c. 1418 mm per year ($z = -2.512$, $P = 0.0077$; Fig. A in Supplementary material), which differentiated between sites for which the species tended to be rarer (mean proportional occurrence = 0.052) and sites for which the species were commoner (mean proportional occurrence = 0.276). There were sites in the sub-optimal climatic zone with higher occurrence values explained by favourable habitat quality, e.g. aspen stands, while some sites in the optimal climatic zone had lower occurrence values, explained by their less suitable habitat quality, e.g. coniferous pinewood sites (Kuusinen, 1996). Values for annual precipitation were significantly correlated with mean temperature of the coldest month ($r = 0.44$, $P < 0.05$ with 18 df).

3.1. Niche modelling

Niche modelling for the optimal and sub-optimal climatic zones generated two statistically significant NPMR models, to explain likelihood of occurrence for cyanolichen and tripartite epiphytes using microhabitat variables. The explanatory variables were contrasting among the two different regions (Table 1; Fig. 3); for the optimal climatic zone, including tree species identity and size (girth), and for the sub-optimal climatic zone, including tree species identity and the presence-absence of bryophytes. In general terms, the response models showed that epiphyte occurrence increased with tree size/age (optimal zone), and in the presence of co-occurring bryophytes (sub-optimal zone), though with higher occurrence values for certain tree species such as *Corylus avellana*, *Fraxinus excelsior* and *Sorbus aucuparia*, compared to *Alnus glutinosa*, *Betula* spp. and *Pinus sylvestris*.

The 'least training presence' was used as a threshold to discriminate between suitable and unsuitable microhabitat. Threshold values in modelled likelihood of occurrence were set at 0.0294 or 0.04651, for the optimal and sub-optimal zones, respectively. This demonstrated two important contrasts among the zones (Fig. 4): 1. There was a greater proportion of potentially suitable microhabitat in the optimal (80%) compared to the sub-optimal climatic zone (47.5%), and 2. Of this suitable microhabitat, more was occupied in the optimal (32.4%) compared to the sub-optimal climatic zone (14.2%), providing field estimates for the value *P*' in the population simulation (proportion of suitable microhabitat occupied).

Table 1
Diagnostics for NPMR models that best explained the response of cyanolichen and tripartite epiphytes in optimal and sub-optimal climatic zones (cf. Fig. 3).

Climatic Zone	Explanatory Variables	Tolerance	Sensitivity	log*B*	$P_{MC(250)}$	AUC
Optimal	Tree species identity	NA	NA	36.37	< 0.005	0.848
	Tree girth (size/age)	67.75	0.27			
Sub-optimal	Tree species identity	NA	NA	14.15	< 0.005	0.789
	Bryophyte occurrence	NA	NA			

Tolerance = the width of a local smoother expressed as units of the environmental data range; Sensitivity = the mean shift in the response variable (as a proportion of its range) given a 5% shift in the explanatory variable; log*B* = the log-likelihood ratio; P_{MC} = significance under a permutation test; AUC = area under the receiver operating curve. Note that the tolerance and sensitivity are not applied to categorical variables.

3.2. Population simulation

The proportion of suitable microhabitat estimated from the field sampled data (0.8 and 0.475) formed the value *K* for optimal and sub-optimal climatic zones. The proportional occupancy of suitable microhabitat (*P*' = 0.324 and 0.142) was then used to identify the values of *Cl* (colonisation rate) that reconstruct *P*' for each zone (Fig. B in Supplementary material). Focussing on values of *K* and *Gt* relevant to the contrasting optimal and sub-optimal zones, the population simulation showed that it was necessary to invoke a higher overall colonisation rate (combinatorial values of *Cl* and $_mP$) for the sub-optimal relative to the optimal zone (Fig. C in Supplementary material) in order to reconstruct their respective values of *P*'. This was found to be the case despite the lower percent occupancy of suitable microhabitat in the sub-optimal climatic zone. In the optimal climatic zone, for a situation where $_mP = 0$ (no rescue effect), the colonisation rate (*Cl*) required to recreate *P*' = 0.324 was equivalent to 0.118 propagules achieving colonisation status (i.e. arriving into a suitable or unsuitable microhabitat) per reproductive thallus per time-step (≈ year), or once every 8.5 years per reproductive thallus (Figs. C and D in Supplementary material). In the sub-optimal climatic zone the values required to recreate *P*' = 0.142, were *Cl* = 0.262 or 0.52 for *Gt* = 20 years or 35 years, respectively, or once every 4 years or 2 years per reproductive thallus (Figs. C and D in Supplementary material). Even allowing for differences in the rate of propagule colonisation to reconstruct *P*', the microhabitat age-at-establishment was skewed towards higher values for the sub-optimal climate (Fig. E in Supplementary material): Kruskal-Wallis $\chi^2 = 6.7$, $P = 0.035$ with 2 df.

3.3. Risk scenarios

Scenarios used a value of $_mP$ that was based on the known spatial configuration of ancient woodland and a dilution effect that depended on the distance from potential sources (surrounding ancient woodlands) to a sink (the simulated woodland patch). The mean value of $_mP$ in the optimal climatic zone was 0.0157 ± 0.0047 (± 1 SD), equivalent to a rescue effect that was c. 1.5% of within-patch colonisation events.

These estimated $_mP$ values for oceanic western Scotland were used to determine values of *Cl* under field conditions, and which are therefore required to reconstruct values of *P*' observed for the optimal climatic zone (Fig. C in Supplementary material). Accordingly, a value in which *Cl* = 0.1162 (combined with $_mP = 0.0157$) was used to simulate stochastic population dynamics over 1000 time-steps (t_1-t_{1000}), and following environmental change at t_{1001} proceeding to t_{2000} (equilibrium population size = 2592 individuals, when *H* = 10,000, *K* = 0.8 and *P*' = 0.324). Three key observations emerge from the environmental change scenarios (Fig. 5):

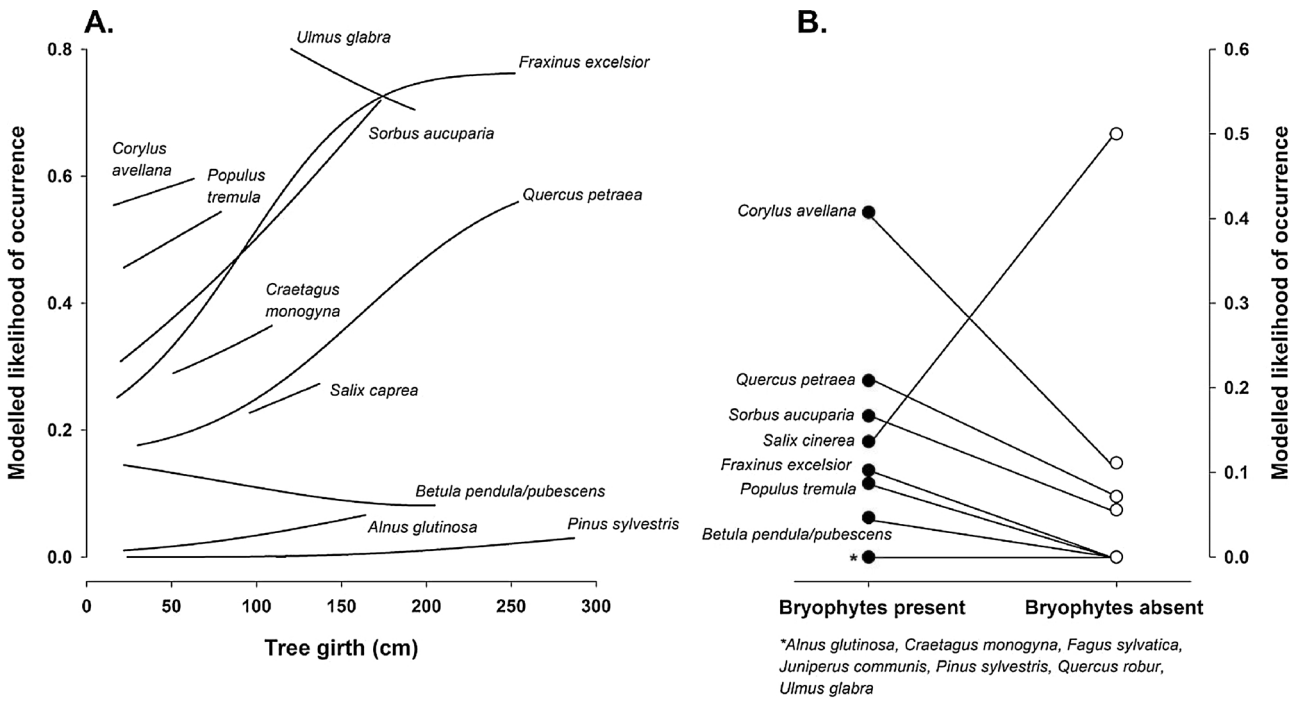

Fig. 3. The niche response (likelihood of occurrence) for cyanolichen and tripartite epiphytes, modelled using NPMR (cf. Table 1). A. In an optimal climatic zone, showing the response to tree girth (size/age) for different tree species, and B. In a sub-optimal climatic zone, showing the effect of bryophyte presence/absence for different tree species.

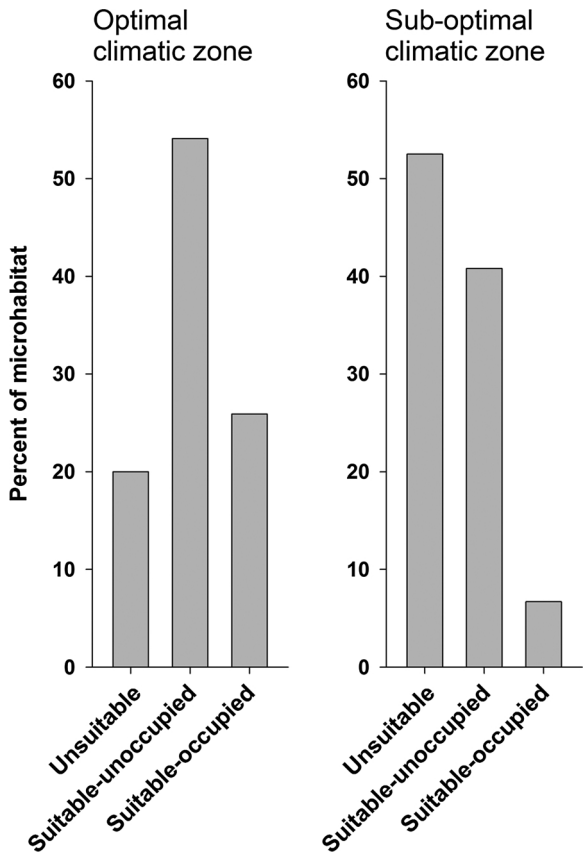

Fig. 4. Based on NPMR niche model results (cf. Table 1, Fig. 3), the percent of unsuitable microhabitat, and suitable-unoccupied and suitable-occupied microhabitat, for trees grouped within the optimal and sub-optimal climatic zones (cf. Fig. A in Supplementary material).

1. A shift towards lower growth rates for cyanolichen and tripartite epiphytes in the optimal climatic zone (longer generation times) decreased the population size (plot i, in Fig. 5 parts A, B and C). With a generation time (*Gt*) of 14 yr the population stabilised and survived in the long-term, but for *Gt* = 20 or 35 yr the population declined to extinction. The decline to extinction is more rapid as the growth to reproductive maturity slows, but even when *Gt* = 35 yr the decline extends over centuries.
2. Reducing the availability of suitable microhabitat increased the rate of population decline towards extinction (plots ii, iii and iv, in Fig. 5 parts A, B and C). Even for a situation where *Gt* increased from as little as 9 yr to 14 yr, an accompanying decline in *K* from 0.8 to 0.6 caused population extinction. This decline to extinction varied from c. ≤200 yr (*Gt* from 9 to 35 yr, and *K* from 0.8 to 0.2) to > 700 yr (*Gt* from 9 to 14 yr, and *K* from 0.8 to 0.6).
3. The negative effect of lower growth rates (increasing *Gt*, see scenario 1., above) can potentially be offset by modifying the availability of suitable microhabitat, or by facilitating a higher rescue effect ($_mP$). For example, given a shift in *Gt* from 9 to 14 yr, increasing *K* from 0.8 to 0.942, or $_mP$ from 0.0157 to 0.276, had the effect of offsetting negative impacts and stabilising the population size (inset graph, Fig. 5 part A).

4. Discussion

The aim of the study was to explore a mechanistic approach in assessing species climate change risk. Differences in the availability of suitable microhabitats for contrasting climates were combined with a functional climatic response in terms of species growth rates and generation times. These effects were implemented through a population simulation model (Appendix A in Supplementary material, and see Ellis (2017)), to explore alternative environmental change scenarios. The model here is a generalizable, heuristic tool, while for specific application (a given species at a given site) output values will require further validation through comparison with independent field data e.g. implementation over multiple different landscapes, to match model outputs with observed species occurrence/abundance. Nevertheless, it uses

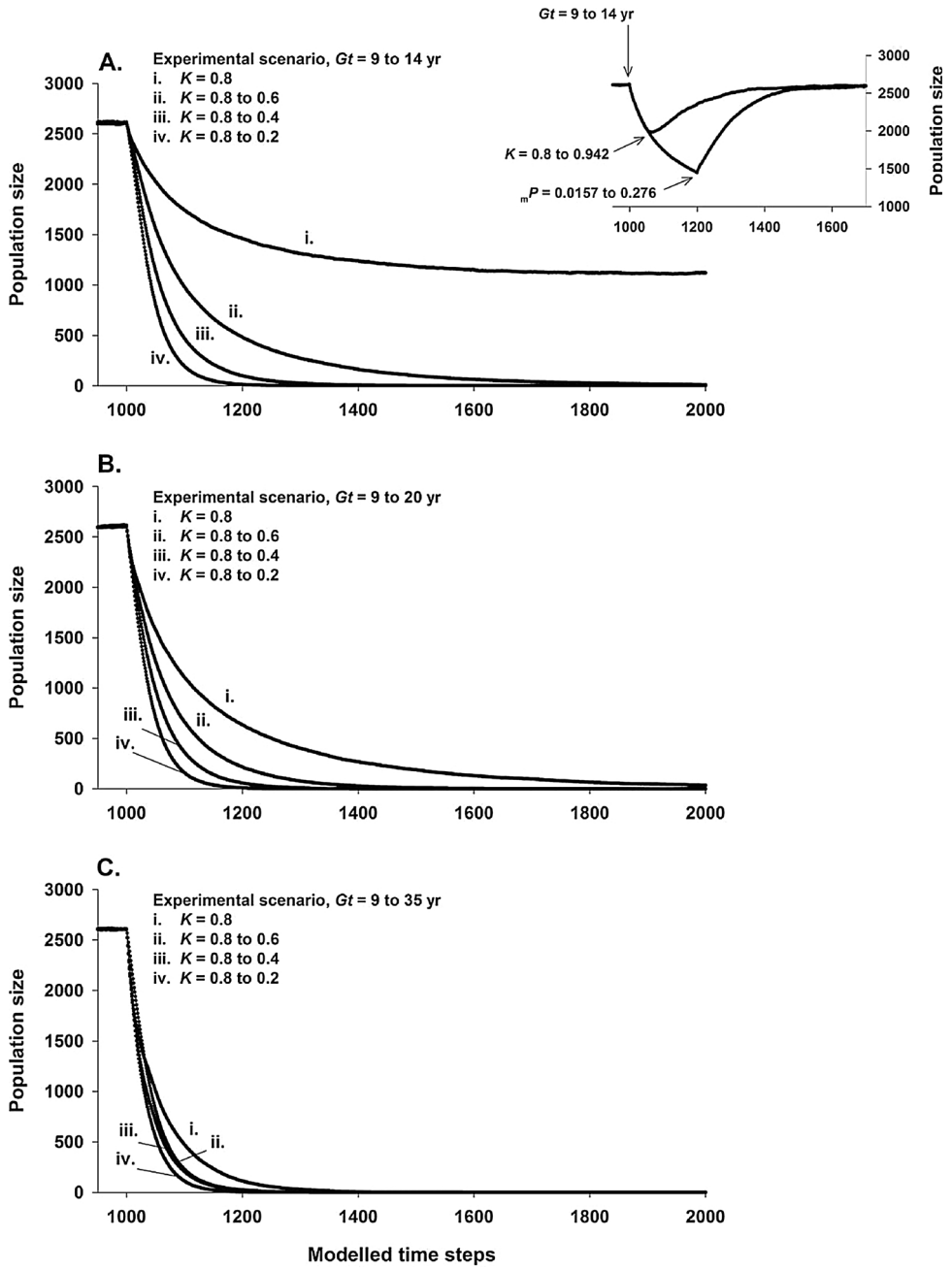
A.
Experimental scenario, Gt = 9 to 14 yr
i. K = 0.8
ii. K = 0.8 to 0.6
iii. K = 0.8 to 0.4
iv. K = 0.8 to 0.2
Gt = 9 to 14 yr
K = 0.8 to 0.942
mP = 0.0157 to 0.276
Population size
B.
Experimental scenario, Gt = 9 to 20 yr
C.
Experimental scenario, Gt = 9 to 35 yr
Modelled time steps

Fig. 5. The effect on the equilibrium population size (population size = 2592, when H = 10,000, K = 0.8, Gt = 9, Cl = 0.1162, with $_mP$ = 0.0157), when Gt (generation time) is lengthened because of slower growth from A. 9 yr to 14 yr, B. to 20 yr and C. to 35 yr. In each case either maintaining K = 0.8, or shifting the proportion of suitable microhabitat downwards to 0.6, 0.4, or 0.2. The inset graph shows resilience options to offset the negative effect of slower growth and longer generation time (for scenario A. from 9 yr to 14 yr) by manipulating K or $_mP$.

biologically realistic population parameters to create testable hypotheses, and this use of the model and scenarios is discussed below.

4.1. *Lobaria pulmonaria* as a model for cyanolichen and tripartite epiphytes

The population biology of lichens is in general poorly known, and in order to make the simulation possible, several demographic parameters were adopted for the well-studied tripartite lichen *Lobaria pulmonaria* (Scheidegger and Werth, 2009). This is one of few lichen epiphytes for which growth rate data are available in different climatic settings (Gaio-Oliveira et al., 2004; Gauslaa et al., 2007). However, to develop a response model that captured the link between macroclimate and microhabitat specificity, field-sampled data had to be combined across multiple cyanolichen and tripartite epiphytes. This leads to an assumption either that the growth rate and generation time of *L. pulmonaria* provide good representations for cyanolichen and tripartite epiphytes generally, or that a response model for cyanolichen and tripartite epiphytes effectively captures the niche response of *L. pulmonaria*.

Related to the first point (similarity in growth rates/generation times), the climatic factors controlling growth rates may be broadly comparable within the cyanolichen and tripartite epiphyte guild (Ellis, 2013; Rikkinen, 2015), including a physiological requirement for direct wetness and warmer temperatures, to support carbon- and/or nitrogen-fixation (Lange et al., 1986; Lange et al., 1993; Antoine, 2004). However, the absolute values for growth rate and size at reproductive maturity are different among cyanolichen and tripartite species (Larsson and Gauslaa, 2011; Hilmo et al., 2013). Thus, growth rate and

generation time for *L. pulmonaria* will reconstruct only in relative terms a climatic-sensitivity for cyanolichen and tripartite epiphytes. Related to the second point (similarity in niche requirements) it is likely that the response model for cyanolichen and tripartite epiphytes is a good general representation of that for *L. pulmonaria*. This is based on three observations. First, although *L. pulmonaria* was too infrequent over the 1013 quadrats to generate a robust niche model for itself, it was the most frequently occurring of the cyanolichen and tripartite species (cf. Table A in Supplementary material), and thus had a large relative effect on the structure of the final niche model. Second, it has been frequently noted by phytosociologists that *L. pulmonaria* is the dominant species in a community characterised by an association of cyanolichen and tripartite epiphytes with shared niche requirements, referred to as the '*Lobarion*' (Barkman, 1958; James et al., 1977; Rose, 1988). Third, the identity and effect of explanatory variables selected into the optimum NPMR response models (e.g. tree species, tree size (≈age), and bryophyte cover), match very closely with those previously shown to explain the distribution of cyanolichen and tripartite epiphytes (Cleavitt et al., 2009), and in particular *L. pulmonaria* (Jüriado et al., 2012). It is assumed here that the response models, which become statistically tractable by training at a guild-scale, capture reasonably well the niche dynamics of *L. pulmonaria*. However, future work aiming to move the modelling process from the general to the specific would benefit from higher sampling efforts in order to generate individualistic niche responses for species separately.

4.2. Niche dynamics

The development of two response models was based on a statistically significant difference in the proportion of trees occupied for optimal (oceanic: consistently wetter and warmer) and sub-optimal climatic zones (more continental: consistently drier with cooler minimum temperatures). These models were then used to estimate – for each zone – the proportion of microhabitat (≈trees) that was suitable, and the proportion of this suitable microhabitat that was occupied.

The recognition of optimal and sub-optimal climatic zones was consistent with physiological constraints for the cyanolichen and tripartite epiphyte guild (see Lobaria pulmonaria *as a model for Cyanolichen and Tripartite Epiphytes*, above), reflecting increased physiological performance under an oceanic mild and consistently moist climate (Ellis, 2013; Rikkinen, 2015). The response models also indicated that among each of these zones the microhabitat effect had both similarities and differences. Tree species identity was a common factor among climatic zones, and is known to be an important compound variable that integrates the effects of bark texture and chemistry (Kuusinen, 1996; Jüriado et al., 2009; Lewis and Ellis, 2010). Cyanolichen and tripartite epiphytes have been shown to occur more frequently in microhabitats of mesotrophic bark with sub-neutral pH (Gauslaa, 1985; Bates, 1992), explaining their association with certain tree species such as ash (*Fraxinus excelsior*), aspen (*Populus tremula*), elm (*Ulmus* spp.) or rowan (*Sorbus aucuparia*) (Mežaka et al., 2008; Jüriado et al., 2009). However, in the optimal climatic zone, suitable microhabitat included a generally positive effect of tree size, and/or age. This could be explained by age related shifts in tree microhabitats (bark texture/chemistry) favouring a species occurrence (Ellis and Coppins, 2007c; Fritz et al., 2009), but it also indicates the potential importance of a 'neutral' sampling effect for larger/older trees: the mathematical probability of colonisation increasing with tree size, or age. Accordingly, it has been suggested that the neutral effect of tree size/age is of primary importance in explaining the distribution of cyanolichen and tripartite epiphytes on a single highly suitable substratum, aspen (Esseen, 1981; Kuusinen, 1994), within an optimal oceanic climate of south-west Norway (Schei et al., 2013).

The findings here suggest that there is a shift along the climatic gradient between the signature of deterministic niche response and neutral effects. Thus, explored theoretically (Fig. F in Supplementary material), the importance of tree size/age (neutral effect) decreases relative to microhabitat availability (niche response), in relation to the declining proportion of suitable microhabitat following transition from an optimal to sub-optimal climate (cf. Fig. 1). This decrease is balanced by the counter effect of an increasing generation time in sub-optimal climates, which would tend to favour the signature of tree size/age. Notwithstanding the fact that the optimal climatic zone included multiple tree species with varying degrees of suitability (tree species identity), the signature effect of tree size/age may appear stronger under optimal climatic conditions where suitable microhabitat is widely available and niche constraints are less severe.

For the sub-optimal climatic zone, the occurrence of bryophytes added a second deterministic niche response alongside tree identity. It is possible that the occurrence of bryophytes is correlated with that of cyanolichen and tripartite epiphytes because of their similar microhabitat requirements, though it is intriguing that an equivalent correlation is not observed for the optimal climatic zone. Invoking macroclimatic constraints to growth (Eaton and Ellis, 2012; Ellis et al., 2017) the presence of bryophytes may create a facilitation effect, with the more humid microclimate of bryophyte mats (Veneklaas et al., 1990) offering a suitable niche for cyanolichen and tripartite establishment under sub-optimal macroclimatic conditions (Sillett and McCune, 1998; Colesie et al., 2012). The availability of microhabitat 'refugia' in sub-optimal climates – such as humid microclimatic niches (e.g. leaning trees with deeply furrowed-bark, and bryophyte cover) – may be skewed towards older trees occurring in stands that are non-intensively managed or old-growth (Vuidot et al., 2011) explaining an association of oceanic species with ancient woodlands (Ellis et al., 2009). In sub-optimal climates, a deterministic niche response may therefore operate in combination with lower growth rates and longer generation times, to strengthen the importance of microhabitat continuity.

4.3. Population simulation

Population simulation was used to reconstruct the proportional occupancy of suitable microhabitat (*P*'), as a function of microhabitat availability (*K*), using parameters that included a climatically controlled growth rate (*Gt*), combined with within- and between-patch dispersal, given colonisation rates plus connectivity (*Cl* and $_{m}P$), and rates of microhabitat disturbance/extinction (*E*). Measured values for *E* were based on deterministic tree mortality (Peterken, 1996; Drobyshev et al., 2009) and stochastic epiphyte extinction from standing trees (Öckinger and Nilsson, 2010; Fedrowitz et al., 2012), while *Gt* used generation times described for optimal (Eaton and Ellis, 2014), or sub-optimal climates (Scheidegger et al., 1998; Scheidegger and Goward, 2002).

The simulation revealed an important discrepancy. Values of *Cl* (colonisation rate) that were able to reconstruct observed patterns in *P*' suggested that the colonisation rate in the sub-optimal climatic zone must be higher than that for the optimal zone. There appears to be no clear biological reason why this should be the case, comparable for example to phenotypic plasticity and increased reproductive output for stressful environments observed in guilds such as annual vascular plants (Aronson et al., 1993; Petrů et al., 2006). An alternative explanation is some form of model mis-parameterization that would otherwise allow values of *P*' to be reconstructed at a lower colonisation rate. For example, the disturbance rate (*E*) causing epiphyte extinction could be different among the climatic zones, i.e. lower disturbance for the sub-optimal zone, though again there appears to be no current evidence as to why this should be the case. Alternatively, growth rates may be faster in the sub-optimal climatic zone than anticipated (< 20–35 yr). However, even with the colonisation rate and generation time for the sub-optimal climatic zone equivalent to those in the optimal zone ($Cl = 0.118$, $Gt = 9$), reconstructed values of *P*' continued to fall well below the field observed values ($P' = 0.0006 \pm 0.0013$). Other explanations are consistent with the observation that environmental

change (leading to lower *K* or *Gt*) resulted in population decline over long periods of time (possibly several centuries). Given this extended time-lag, the cyanolichen and tripartite epiphyte populations in the sub-optimal climatic zone may represent non-equilibrium conditions: 1. Allowing for past higher epiphyte growth rates during historic periods with more suitable climatic conditions (Ellis et al., 2014b), 2. Having responded to a period when woodland structure was more diverse, and values of *K* were therefore higher, with an ability to sustain larger epiphyte populations at lower colonisation rate (*Cl*), and prior to the extensive simplification of woodland during the 19th Century (Smout et al., 2007), and/or 3. With populations maintained by a high rescue effect (higher $_{m}P$) through dispersal from the optimal climatic zone, during a period when native woodlands had not only greater heterogeneity (higher values of *K*, point 2., above) but also had higher values of connectivity across the landscape (Birks, 1988; Woodbridge et al., 2014). These explanations invoke an extinction debt in the sub-optimal climatic zone (Kuussaari et al., 2009), as has been inferred for lichen epiphytes previously (Berglund and Jonsson, 2005; Johansson et al., 2013b). The extinction debt emerges from the time-lag over which populations attain equilibrium following landscape-scale habitat change, owing to longevity of established individuals (Scheidegger et al., 2000) and low values for microhabitat disturbance and extinction rates. Reanalysis of species richness for cyanolichen and tripartite epiphytes in Scotland (Ellis and Coppins, 2007a) strongly supports this argument (Fig. G in Supplementary material), since the extinction debt appears stronger under sub-optimal compared to optimal climatic conditions. This is consistent with a more delayed response in achieving population equilibrium following landscape change in situations where the growth rate is slower, the generation time longer, the population size smaller, with consequently lower values for the among-patch dispersal of propagules (Ellis, 2017). These temporal characteristics are also critically important in understanding the population response to future environmental change scenarios.

4.4. Species risk and environmental change scenarios

Example scenarios used here explored climate change for an optimal climatic zone (oceanic), as a reduction in epiphyte growth rate, and an increased generation time. This is consistent with research to show that reproduction depends on lichen thallus size for *L. pulmonaria* (Martínez et al., 2012; Hilmo et al., 2013; MacDonald and Coxson, 2013) with juvenile growth rates controlled by macroclimate (Eaton and Ellis, 2012) as is demonstrated experimentally (Larsson and Gauslaa, 2011; Merinero et al., 2015). However, it is not yet fully clear how climate change will affect cyanolichen and tripartite epiphytes. Some bioclimatic models based on summary climate variables have indicated increased suitability for oceanic epiphytes (Ellis and Coppins, 2007b; Ellis et al., 2007b), for regions with warming temperatures and consistent wetness. However, the climate will undergo shifts in seasonal patterns of rainfall which may amplify during the 21st Century, including for the study region of oceanic western Scotland (Jenkins et al., 2010; Werritty and Sugden, 2012). The combination of a seasonal climatic effect with patterns of solar insolation (Reu et al., 2014) may lead to negative outcomes if increased wetness during winter cause higher rates of respiration (high physiological activity for hydrated lichens, though during low light levels), which is not then compensated during the dryness of summer months (low physiological activity for desiccated thalli, though during higher light levels). Previous work has demonstrated the sensitivity of lichen growth to seasonal patterns of temperature, humidity and solar insolation (Muir et al., 1997; Larsson et al., 2012), and preliminary analyses have suggested that this intra-annual variation will be important in understanding the lichen physiological response to projected climate change (Čabrajić, 2009; Ellis et al., 2017).

Assuming the epiphyte response is not determined by catastrophic thresholds, a gradual climate change impact on growth rates will be subject to a time-lag in affecting population equilibrium, as has been observed for epiphyte metapopulations (Johansson et al., 2013a). Availability of suitable microhabitat (*K*), or the connectivity of landscape-scale habitat contributing to a rescue effect ($_{m}P$), could in principle be managed upwards over decades or centuries, so as to offset the negative consequences of lower growth rates and longer generation times (*Gt*). In the example provided here, an increased microhabitat suitability would require higher proportions of older/larger dominant tree species such as ash (*Fraxinus excelsior*), aspen (*Populus tremula*) or oak (*Quercus petraea*), and sub-dominants such as hazel (*Corylus avellana*) or rowan (*Sorbus aucuparia*), or else an increase in the landscape extent of ancient/old-growth woodland from 1.5% to > 25% cover in the landscape. However, combining multiple impacts such as climate change with a catastrophic loss of suitable habitat, such as might occur during a tree disease scenario (Jönsson and Thor, 2012; Lõhmus and Runnel, 2014), creates urgency in conservation to address multiple potential threats (Ellis et al., 2014a). In the simulation model these interacting threats greatly increased the magnitude of and accelerated epiphyte population decline, shortening the window of opportunity for effective action. This window may shift from over 700 yr to less than 200 yr. When considering the length of time that is required to reconstruct suitable habitat for old-growth epiphytes – veteran trees in ancient woodlands – the use of scenarios becomes essential for conservation planning that is sensitive to realistically long ecological timescales.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ppees.2018.02.003.

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